

- FIGS. 6a, 6b. "*Turbo*" *sulcostomus*, Phillips. Kelloway Rock, Scarborough. Leckenby Collection. Front and back view.
 ,, 7. "*Turbo*" *sulcostomus*, Phillips. Kelloway Rock. ? Hackness. British Museum.
 ,, 8. *Amberleya clavata*, Bean, MS. Oxford Clay, Scarborough. British Museum.
 ,, 9a, b, c. *Littorina biserta*, Phillips. Dogger, Blue Wyke. Leckenby Collection. Front, back, and portion enlarged.
 ,, 10a, b, c. ,, var. *unicarinata*, Bean. Dogger, Blue Wyke. Leckenby Collection. Front, back, and portion enlarged.
 ,, 11a, b, c. *Amberleya biserta*. Dogger, Blue Wyke. Jermyn Street Museum. Front, back, and portion enlarged.
 ,, 12, 12a. "*Turbo melanioides*," Bean, MS. Dogger, Blue Wyke. York Museum. Front view, and *facsimile* of aperture.

II.—THE PRINCIPAL CHARACTERS OF AMERICAN JURASSIC DINOSAURS BELONGING TO THE ORDER THEROPODA.¹

By PROFESSOR O. C. MARSH, M.A., F.G.S.

Of Yale College, Newhaven, Ct., U.S.A.

THE carnivorous *Dinosauria* form a well-marked order, which the writer has called the *Theropoda*, in his classification of this group.² Although much has been written about these reptiles since Buckland described *Megalosaurus* in 1824, but little has really been made out in regard to the structure of the skull, and many portions of the skeleton still remain to be determined.

The fortunate discovery of two nearly perfect skeletons of this order, as well as a number of others with various important parts of the skeleton in good preservation, has afforded the writer an opportunity to investigate the group, and some of the results are here presented. A more detailed description of these fossils, and others allied to them, will be given in another communication.

Of the carnivorous Dinosaurs from the American Jurassic, there are four genera, which each represents, apparently, a distinct family. These genera are *Allosaurus*, *Cœlurus*, *Labrosaurus*, and the new genus *Ceratosaurus*, here described. In the present article, *Allosaurus* and *Ceratosaurus* will be mainly used to illustrate the more important characters of the order, and the relations of the other genera to them will be indicated in the classification presented in conclusion.

The specimen of *Ceratosaurus* here first described presents several characters not hitherto seen in the *Dinosauria*. One of these is a large horn on the skull; another is a new type of vertebra, as strange as it is unexpected; and a third is seen in the pelvis, which has the bones all cœssified, as in existing Birds. *Archæopteryx* alone among adult birds has the pelvic bones separate, and this specimen of *Ceratosaurus* is the first Dinosaur found with all the pelvic bones ankylosed. Another feature of this skeleton, not before seen in the *Theropoda*, is the presence of osseous dermal plates. These extend from the base of the skull along the neck, over the vertebræ. The plates appear to be ossified cartilage.

¹ From the American Journal of Science, vol. xxvii. April, 1884.

² Silliman's Journal, vol. xxiii. p. 81, January, 1882. See also vol. xxi. p. 423, May, 1881; p. 339, April, 1881; and vol. xvii. p. 89, January, 1879.

This interesting fossil is quite distinct from any hitherto described, and, as it represents a new genus and species, may be called *Ceratosaurus nasicornis*. It also belongs to a new family, which may be named the *Ceratosauridæ*.

The skeleton, which is almost perfect, is over seventeen feet in length by actual measurement. The animal when alive was about half the bulk of the species named by the writer *Allosaurus fragilis*, which is from the same geological horizon. A second skeleton, some parts of which, also, are here described, is referred to the latter species.

THE SKULL.—The skull of *Ceratosaurus nasicornis* is very large, in proportion to the rest of the skeleton. The posterior region is elevated, and moderately expanded transversely. The facial portion is elongate, and tapers gradually to the muzzle. Seen from above, the skull resembles in general outline that of a crocodile. The nasal openings are separate, and lateral, and are placed near the end of the snout, as shown in Fig. 1.

Seen from the side, this skull appears Lacertilian in type, the general structure being light and open. From this point of view, one special feature of the skull is the large, elevated, trenchant horn-core, situated on the nasals (Fig. 1, *b*). Another feature is the large openings on the side of the skull, four in number. The first of these is the anterior nasal orifice (*a*); the second, the very large triangular antorbital foramen (*c*); the third, the large oval orbit (*d*); and the fourth, the still larger lower temporal opening (*e*). A fifth aperture, shown in the top view of the skull, is the supra-temporal fossa. These openings are all characteristic of the *Theropoda*, and are found also in the *Sauropoda*, but the antorbital foramen is not known in any of the other *Dinosauria*.

The plane of the occiput, as bounded laterally by the quadrates, is inclined forward. The quadrates are strongly inclined backward, thus forming a marked contrast to the corresponding bones in *Diplodocus*, and the other *Sauropoda*. The occipital condyle is hemispherical in general form, and is somewhat inclined backward, making a slight angle with the long axis of the skull. The basi-occipital processes are short, and stout. The par-occipital processes are elongate and flattened, and but little expanded at their extremities. They extend outward and downward, to join the head of the quadrate.

The hyoid bones appear to be four in number. They are elongate, rod-like bones, somewhat curved, and in the present specimen were found near their original position.

The parietal bones are of moderate size, and there is no parietal foramen. The median suture between the parietals is obliterated, but that between these bones and the frontals is distinct.

The frontal bones are of moderate length, and are closely united on the median line, the suture being obliterated. Their union with the nasals is apparent on close inspection.

The nasal bones are more elongate than the frontals, and the suture uniting the two moieties is obsolete. These bones support entirely the large compressed, elevated horn-core, on the median

line. The lateral surface of this elevation is very rugose, and furrowed with vascular grooves. It evidently supported a high, trenchant horn, which must have formed a most powerful weapon for offence and defence. No similar weapon is known in any of the *Dinosauria*, but it is not yet certain whether this feature pertained to all the members of this family, or was only a generic character.¹

The premaxillaries are separate, and each contained only three functional teeth. In the genera *Compsognathus* and *Megalosaurus*, of this order, each premaxillary contained four teeth, the same number found in the *Sauropoda*. In the genus *Creosaurus*, from the American Jurassic, the premaxillaries each contain five teeth.

The maxillary bones in the present specimen are large and massive, as shown in Fig. 1. They unite, in front, with the premaxillaries by an open suture; with the nasals, laterally, by a close union; and, with the jugal behind, by squamosal suture. The maxillaries are provided each with fifteen functional teeth, which are large, powerful, and trenchant, indicating clearly the ferocious character of the animal when alive. These teeth have the same general form as those of *Megalosaurus*, and the dental succession appears to be quite the same.

Above the antorbital foramen on either side, is a high elevation composed of the prefrontal bones. These protuberances would be of service in protecting the orbit, which they partially overhang.

The orbit is of moderate size, oval in outline, with the apex below. It is bounded in front by the lachrymal, above this by the prefrontal, and at the summit the frontal forms for a short distance the orbital border. The post-frontal bounds the orbit behind, but below, the jugal completes the outline.

The jugal bone is L-shaped, the upper branch joining the post-frontal, the anterior branch uniting with the lachrymal, above, and the maxillary below. The posterior branch passes beneath the quadrato-jugal, and with that bone completes the lower temporal arch, which is present in all known Dinosaurs.

The quadrato-jugal is an L-shaped bone, and its anterior branch is united with the jugal by a close suture. The vertical branch is closely joined to the outer face of the quadrate.

The quadrate is very long, and compressed antero-posteriorly. The head is of moderate size, and is enclosed in the squamosal. The lower extremity of the quadrate has a double articular face, as in some birds. One peculiar feature of the quadrate is a strong hook, on the upper half of the outer surface. Into this hook of the quadrate, a peculiar process of the quadrato-jugal is inserted, as shown in Fig. 1.

The pterygoid bones are very large, and extend well forward. The posterior extremity is applied closely to the inner side of the quadrate. The middle part forms a pocket, into which the lower extremity of the basi-ptyergoid process is inserted. To the lower

¹ The "horn" of *Iguanodon* described by Mantell, and since regarded as a carpal spine, proves to be the distal phalange of the thumb.

FIG. 1.

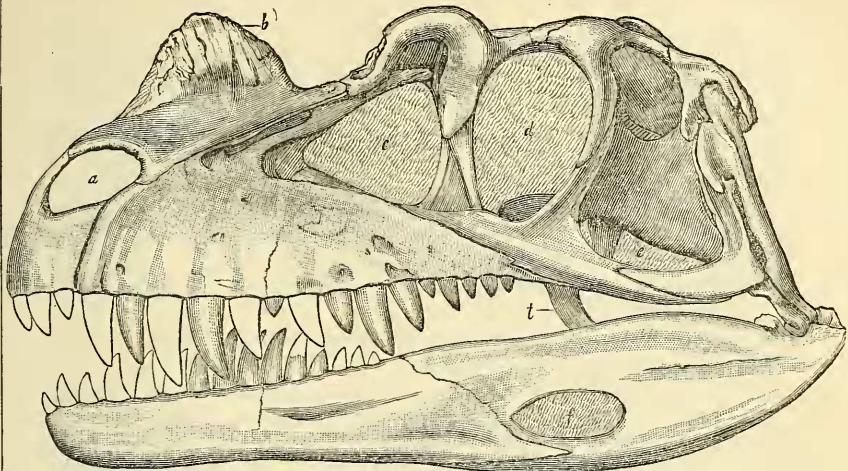


FIG. 2.

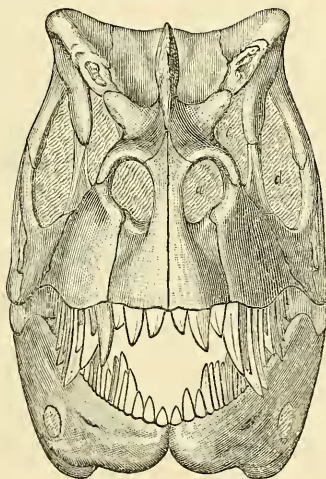


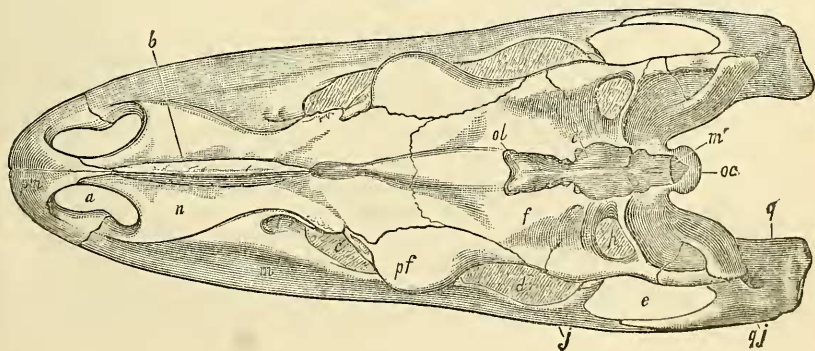
FIG. 1.—Skull of *Ceratosaurus nasicornis*, Marsh; side view.

FIG. 2.—The same skull; front view.

FIG. 3.—Skull and brain-cast of *Ceratosaurus nasicornis*, Marsh; seen from above, one-sixth natural size. *a*, nasal opening; *b*, horn-core; *e*, antorbital opening; *e'*,

cerebral hemispheres; *d*, orbit; *e*, lower temporal fossa; *f*, frontal bone; *h*, supra-temporal fossa; *j*, jugal bone; *m*, maxillary bone; *m'*, medulla; *n*, nasal bone; *oc*, occipital condyle; *ol*, olfactory lobes; *pf*, pre-frontal bone; *pm*, pre-maxillary bone; *q*, quadrate bone; *qi*, quadrato-jugal bone.

FIG. 3.



margin of the pterygoid is united the strong, curved, transverse bone, which projects downward below the border of the upper jaws, as shown in Figure 1, *t*.

There is a very short, thin, columella, which below is closely united to the pterygoid by suture, and above fits into a small depression of the post-frontal.

The palatine bones are well developed and, after joining the pterygoids, extend forward to the union with the vomers. The latter are apparently of moderate size.

The pre-sphenoid is well developed, and has a long pointed anterior extremity.

The whole palate is remarkably open, and the principal bones composing it stand nearly vertical, as in the *Sauropoda*.

THE BRAIN.—The brain in *Ceratosaurus* was of medium size, but comparatively much larger than in the herbivorous Dinosaurs. It was quite elongate, and situated somewhat obliquely in the cranium, the posterior end being inclined downward. The position of the brain in the skull, and its relative size, is shown in Fig. 3.

The foramen magnum is small. The cerebellum was of moderate size. The optic lobes were well developed, and proportionally larger than the hemispheres. The olfactory lobes were large, and expanded. The pituitary body appears to have been very large.

THE LOWER JAWS.—The lower jaws of *Ceratosaurus* are large and powerful, especially in the posterior part. In front, the rami are much compressed, and they were joined together by cartilage only, as in all Dinosaurs. There is a large foramen in the jaw, similar to that in the crocodile, as shown in Fig. 1, *f*. The dentary bone extends back to the middle of this foramen. The splenial is large, extending from the foramen forward to the symphyseal surface, and forming in this region a border to the upper margin of the dentary. There were fifteen teeth in each ramus, similar in form to those of the upper jaws.

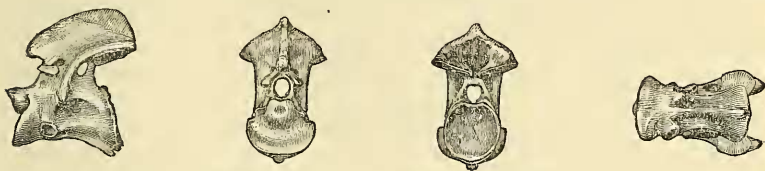
A peculiar dentary bone, recently found, and here referred to *Labrosaurus*, is edentulous in front, and the posterior portion is much decurved. The teeth are more triangular than in the other genera of this order. The species it represents may be called *Labrosaurus ferox*.

THE VERTEBRÆ.—The cervical vertebræ of *Ceratosaurus* differ in type from those in any other known Reptiles. With the exception of the atlas, all are strongly opisthocelien, the cup on the posterior end of each centrum being unusually deep. In place of an equally developed ball on the anterior end, there is a perfectly flat surface. The size of the latter is such that it can only be inserted a short distance in the adjoining cup, and this distance is accurately marked on the centrum by a narrow articular border, just back of the flat anterior face. This peculiar articulation leaves more than three-fourths of the cup unoccupied by the succeeding vertebra, forming, apparently, a weak joint. This feature is shown in Fig. 4.

The discovery of this new form of vertebra shows that the terms opisthocelien and procœlian, in general use to describe the centra

of vertebræ, are inadequate, since they relate to one end only, the other being supposed to correspond in form. The terms convexo-concave, concavo-convex, plano-concave, etc., would be more accurate, and equally euphonious.

FIG. 4.

Axis vertebra of *Ceratosaurus nasicornis*.

In *Ceratosaurus*, as in all the *Theropoda*, except *Cælorus*, the cervical ribs are articulated to the centra, not coössified with them, as in the *Sauropoda*. The latter order stands almost alone among Dinosaurs in this respect, as both the *Stegosauria* and the *Ornithopoda* have free ribs in the cervical region.

The dorsal and lumbar vertebræ are bi-concave, with only moderate concavities. The sides and lower surface of the centra are deeply excavated, except at the ends. These vertebræ show the diplospheal articulation seen in *Megalosaurus*, and also in *Creosaurus*.

All the pre-sacral vertebra are very hollow, and this is also true of the anterior caudals.

There are five well-coössified vertebræ in the sacrum in the present specimen of *Ceratosaurus nasicornis*. The transverse processes are very short, each supported by two vertebræ, and they do not meet at their distal ends.

In the type specimen of *Creosaurus*, there are only two sacral vertebræ coössified. In the *Megalosaurus*, there are five, and the number appears to vary in different genera of the *Theropoda*, as it does in the *Sauropoda*.

The caudal vertebræ are bi-concave. All the anterior caudals, except the first, supported very long chevrons, indicating a high, thin tail, well adapted to swimming. The tail was quite long, and the distal caudals were very short.

THE FORE LIMBS.—The fore limbs in *Allosaurus*, and in fact in all known *Theropoda*, were very small. The scapula and coracoid resembled those of *Megalosaurus*. The humerus was short, and somewhat sigmoid in form. The shaft was hollow, as in all the limb bones of this genus. The manus was peculiar in having some of its digits armed with powerful compressive claws, which formed most effective weapons. These claws, in some allied forms, have been referred to the hind feet, but the latter, in all the known *Theropoda*, have their claws round, and not compressed. The fore limb of *Allosaurus fragilis* is shown in Fig. 8.

THE PELVIC ARCH.—The pelvic bones in the *Theropoda* have been more generally misunderstood than any other portion of the skeleton in Dinosaurs. The ilia, long considered coracoids, have been since usually reversed in position; the ischia have been regarded

as pubes; while the pubes themselves have not been considered as part of the pelvic arch.

Fortunately, in the present specimen of *Ceratosaurus*, the ilium, ischium, and pubes are firmly coössified, so that their identification and relative positions cannot be called in question. The ilia, moreover, were attached to the sacrum, which was in its natural place in the skeleton, and the latter was found nearly in the position in which the animal died. The pelves of *Ceratosaurus* and of *Allosaurus* are shown in Figs. 5 and 6.

The ilium in *Ceratosaurus* has the same general form as in *Megalosaurus*. In most of the other *Theropoda*, also, this bone has essentially the same shape, and this type may be regarded as characteristic of the order. In *Creosaurus*, the anterior wing is more elevated, and the emargination below it wider, but this may in part be due to the imperfection of the border.

The ischia in *Ceratosaurus* are comparatively slender. They project well backward, and for the last half of their length the two are in close apposition. The distal ends are coössified, and expanded.

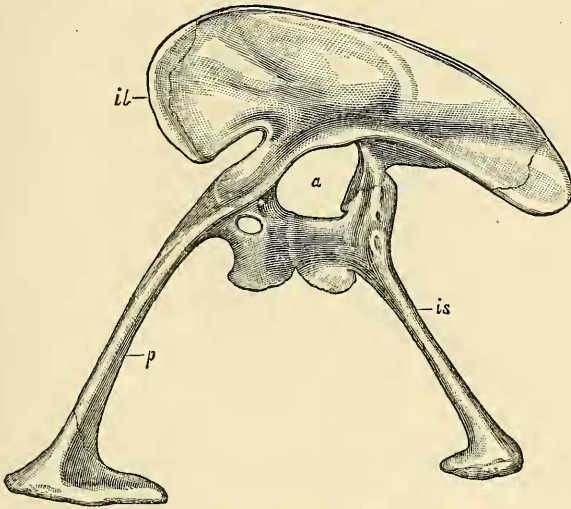
The pubes in *Ceratosaurus* have their distal ends coössified, as in all the known *Theropoda*. They project downward and forward, and their position in the pelvis is shown in Figs. 5 and 6. Seen from the front, they form a Y-shaped figure, which varies in form in different genera. The upper end joins the ilium by a large surface, and the ischium by a smaller attachment. The united distal ends are expanded into an elongate, massive foot, as shown in Figs. 5 and 6, which is one of the most peculiar and characteristic parts of the skeleton.

The pubes of *Megalosaurus* have not yet been identified, but there can be little doubt that they are of the same general type as in *Ceratosaurus* and *Allosaurus*. The pubes of *Cœlurus* pertain to a new species, which may be called *Cœlurus agilis*. This animal was at least three times the bulk of the type. Owen has figured the pubes of another species of this genus, under the name *Poikilopleuron pusillus*, but he regarded the specimen as an "abdominal hæmapophysis and hæmal spine." (Palæontographical Society, vol. xxx. plate i. 1876.)

The extremely narrow pelvis is one of the most marked features in this entire group, being in striking contrast to the width in this region in the herbivorous forms found with them. If the *Theropoda* were viviparous, which some known facts seem to indicate, one difficulty, naturally suggested in the case of a reptile, is removed.

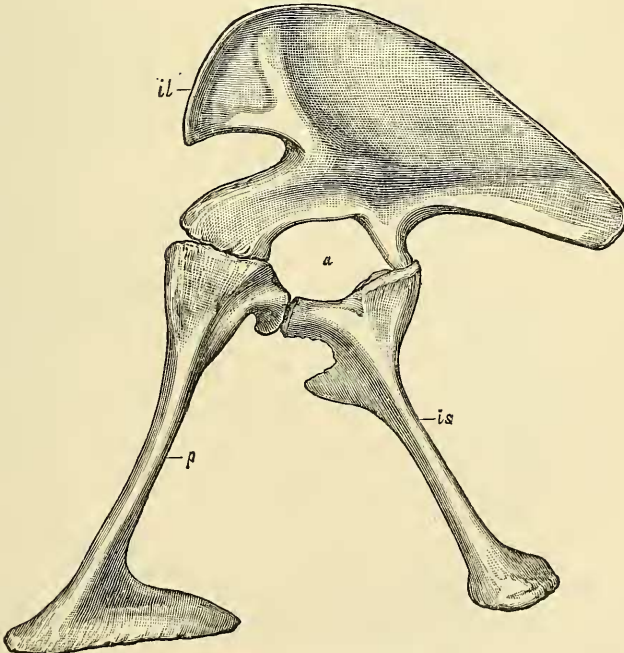
Another interesting point is, the use of the large foot at the lower end of the pubes, which is the most massive part of the skeleton. The only probable use is, that it served to support the body in sitting down. That some Triassic Dinosaurs sat down on their ischia is proved conclusively by the impressions in the Connecticut River sandstone. In such cases the leg was bent so as to bring the heel to the ground. The same action in the present group would bring the foot of the pubes to the ground, nearly or quite under the centre of gravity of the animal. The legs and ischia would then naturally

FIG. 5.



Pelvis of *Ceratosaurus nasicornis*, Marsh ; side view, seen from the left.

FIG. 6.



Pelvis of *Allosaurus fragilis*, Marsh ; the same view. *a*, acetabulum ;
il, ilium ; *is*, ischium ; *p*, pubis.

. Both figures are one-twelfth natural size.

aid in keeping the body balanced. Possibly this position was assumed habitually by these ferocious biped reptiles, in lying in wait for prey.

THE HIND LIMBS.—Several restorations of the posterior limb of *Megalosaurus* have been attempted, but the imperfect material at hand was not sufficient to ensure entire success. In the restoration of *Allosaurus*, given in Fig. 7, only the bones found together have been placed in position. The relative proportions of the femur and tibia are shown in this figure, and the general structure of the foot. The astragalus and calcaneum are distinct from the tibia and fibula, as in all the known *Theropoda*, although their coalescence has been regarded as certain in some of the genera.¹

In the foot of *Allosaurus fragilis*, represented in Fig. 7, no tarsal bones of the second row were found, although the adjoining bones were nearly in their natural position. Whether the former were imperfectly ossified, or lost, in this instance cannot be determined with certainty, but there is evidence of the presence of these bones in several other members of the group. In the present foot, there were three functional digits. The metatarsals are very long, and fitted closely to each other, especially at their upper ends. The phalanges and claws were mostly found near the positions here assigned to them.

The specimens of *Theropoda* here first described, including the type specimen of *Ceratosaurus nasicornis*, are from the Atlantosaurus beds of the Upper Jurassic, in Colorado, where they were found by Mr. M. P. Felch. The associated fossils are various *Sauropoda*, *Stegosauria*, and *Ornithopoda*, together with Jurassic Mammals.²

CLASSIFICATION.

The main characters of the order *Theropoda* and of the families now known to belong to it, are as follows:—

Order THEROPODA.

Premaxillary bones with teeth. Anterior nares at end of skull. Large antorbital opening. Vertebrae more or less hollow. Fore limbs very small; limb bones hollow. Feet digitigrade; digits with prehensile claws. Pubes projecting downward, with distal ends coössified.

- (1.) Family *Megalosauridae*. Anterior vertebrae convexo-concave; remaining vertebrae bi-concave. Pubes slender. Astragalus with ascending process.

Genera, *Megalosaurus* (*Poikilopleuron*), *Allosaurus*, *Celosaurus*, *Creosaurus*, *Dryptosaurus* (*Laelaps*).

- (2.) Family *Ceratosauridae*. Horn on skull. Cervical vertebrae plano-concave, remaining vertebrae bi-concave. Pubes slender. Pelvic bones coössified. Osseous dermal plates. Astragalus with ascending process.

Genus, *Ceratosaurus*.

¹ *Compsognathus* is cited as an instance of this union, but in a careful study of the original specimen in Munich, the writer found evidence that the astragalus is distinct, although closely attached to the tibia. Baur has since proved this conclusively (*Morpholog. Jahrbuch*, viii.). In the *Stegosauridae* alone, among known Dinosaurs, is the astragalus coössified with the tibia. This, however, is not a character of much importance.

² The presence of various genera of Dinosaurs closely allied to these American forms in essentially one horizon in the Isle of Wight, suggests that the beds in which they occur are not Wealden, as generally supposed, but Jurassic.

FIG. 7.

FIG. 7.—Bones of left hind
leg of *Allosaurus fragilis*,
Marsh.

FIG. 8.—Bones of left fore
leg of *Allosaurus fragilis*.

Both figures are one-twelfth
natural size.

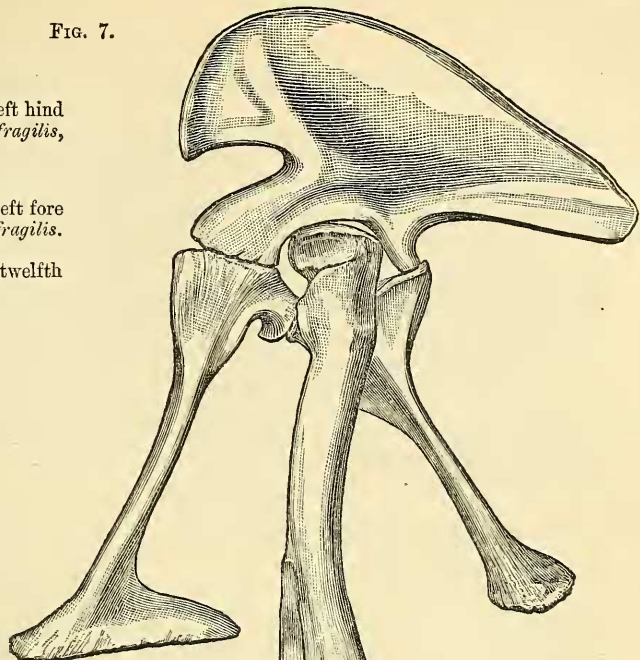
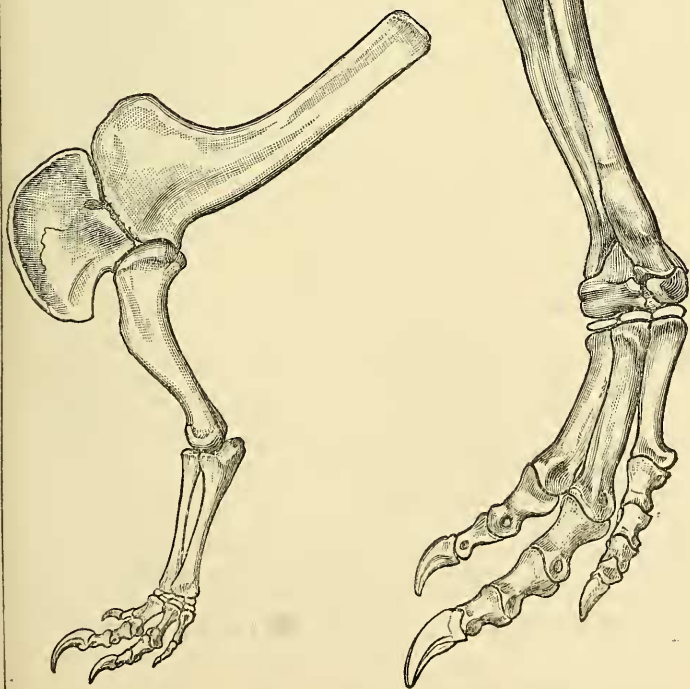


FIG. 8.



- (3.) Family *Labrosauridæ*. Lower jaws edentulous in front. Cervical and dorsal vertebræ convexo-concave. Pubes slender, with anterior margins united. Astragalus with ascending process.
Genus, *Labrosaurus*.
- (4.) Family *Zanclodontidæ*. Vertebræ bi-concave. Pubes broad elongate plates, with anterior margins united. Astragalus without ascending process. Five digits in manus and pes.
Genera, *Zanclodon*, ? *Teratosaurus*.
- (5.) Family *Amphisauridæ*. Vertebræ bi-concave. Pubes rod-like. Five digits in manus, and three in pes.
Genera, *Amphisaurus* (*Megadactylus*), ? *Bathynathus*, ? *Clepsysaurus*, *Palæosaurus*, *Thecodontosaurus*.

Sub-order CÆLURIA.

- (6.) Family *Cæluridæ*. Vertebræ and bones of skeleton pneumatic. Anterior cervicals convexo-concave; remaining vertebræ bi-concave. Cervical ribs coössified with vertebræ. Metatarsals very long and slender.
Genus, *Cælorus*.

Sub-order COMPSOGNATHA.

- (7.) Family *Compsognathidæ*. Cervical vertebræ convexo-concave; remaining vertebræ bi-concave. Three functional digits in manus and pes. Ischia with long symphysis on median line.
Genus, *Compsognathus*.

Of these seven well-marked families, the *Amphisauridæ* and *Zanclodontidæ* are Triassic, the *Megalosauridæ* are Jurassic and Cretaceous, while the others are all Jurassic alone.

There are still some very diminutive carnivorous Dinosaurs that cannot at present be referred to any of the above families; but this may in part be due to the fragmentary condition in which their remains have been found.

The peculiar orders *Hallopoda* and *Aëtosauria* include carnivorous reptiles which are allied to the *Dinosauria*, but they differ from that group in some of its most characteristic features. In both *Aëtosaurus* and *Hallopus*, the calcaneum is much produced backwards. In the former genus, the entire limbs are crocodilian, and this is also true of the dermal covering. In *Hallopus*, the calcaneum is greatly lengthened, and the whole posterior limb is especially adapted to leaping. In both of these genera, there are but two sacral vertebræ, but this may be the case in true Dinosaurs, especially from the Trias. Future discoveries will probably bring to light intermediate forms between these orders and the typical Dinosaurs.

III.—LAND SHELLS IN THE RED CRAG.

By ROBERT G. BELL, F.G.S.

PERHAPS very few Tertiary formations have received a greater amount of attention from geologists and collectors of fossils, during the last forty years, than the Red Crag of Suffolk and Walton-Naze; and it seems singular that so few traces of land life have resulted from so much research. Although in its southern portions it is strictly a marine deposit, yet its distance from shore could not have been very great at any point; but putting aside the few plants and mammalian remains, most of which in the coprolite portion of the Red Crag are derivative, there is little evidence of its proximity.

In that part of Suffolk near Chillesford and around the small